When Abnormality Becomes Perennial in a Reduced Population: The Case of *Altudostephanus longicostis* gen. et sp. nov. (Valanginian Ammonites, South-Eastern France)

Didier Bert 1,2,3,*, Stéphane Bersac 3, Bernard Beltran 3 and Léon Canut 3

1 Réserve Naturelle Nationale Géologique de Haute-Provence, Conseil Départemental des Alpes de Haute-Provence, 13 rue du Docteur Romieu, CS 70216, 04995 Digne-Les-Bains Cedex 9, France
2 Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France
3 Laboratoire du Groupe de Recherche en Paléobiologie et Biostratigraphie des Ammonites (GPA), 65 Grand rue, 04170 La Mure-Argens, France
* Correspondence: didier.paleo@gmail.com

Abstract: The discovery of the new ammonite *Altudostephanus longicostis* gen. et sp. nov. around the lower/upper Valanginian boundary (Lower Cretaceous) with a true longitudinal ribs pattern oriented in the direction of coiling is reported here for the first time for the Cretaceous. This character raises questions as this type of ornamentation is mainly represented in the Paleozoic or old Mesozoic taxa. Its study shows that it is not a ‘shell accident’ and that it belongs to a particular lineage of Olcostephaninae, in a restricted geographical area and in a progenetic evolutionary context derived from *Olcostephanus*, which justifies the introduction of the new monophyletic genus *Altudostephanus* gen. nov. The discovery of a specimen of *Passendorferia* sp. (Oxfordian, Upper Jurassic) with the same pattern allows us to consider that this capacity could have a genetic cause. It seems that the fixation of this character, otherwise strongly recessive, in *A. longicostis* gen. et sp. nov. could take place thanks to a founder effect and the drastic numerical reduction in the population. The geological reference section PIG5 (Moriez area, South-Eastern France) is described, and the problem of the conservation of ‘pyritic’ s.l. ammonites is addressed with a proposed methodology allowing their long-term conservation.

Keywords: ammonites; Valanginian; Vocontian Basin; longitudinal ornamentation; genetic drift; reduced population; Hardy–Weinberg’s equilibrium; ‘pyrite’ conservation

1. Introduction

Generally, when ribs are present in the ornamentation of Mesozoic ammonites, they are developed more or less perpendicular to the direction of the coiling. ‘Spiral’ ribs oriented strictly in the direction of the coiling are a characteristic more often found in the Ammonoida of the late Paleozoic, as for example in *Agathiceras* Gemmellaro, 1887, *Paragastrioceras* Tchernow, 1907, or *Altudoceras* Ruzhentsev, 1940. Most of the time, however, longitudinal ornamentation is rather linked to lirae, striae or megastriae in possibly reticulate patterns (e.g., *Lusitanites* Ruzhentsev & Bogoslovskiaia, 1971, *Owenioceras* Miller & Furnish, 1940, or *Strigoniatites* Spath, 1934) and only rarely true ribs, even sometimes very strong (*Epadrianites* Schindewolf, 1931). This type of ornamentation does not seem linked to the morphology of the ammonoid conch, since it concerns platycone shapes, spherococones, involutes with an ogival section, serpenticocones, etc., which can also be extended to other ectocochleate cephalopods, as it includes orthoconic (e.g., *Kionoceras* Hyatt, 1884), cyrtococonic (e.g., *Calocyrtoceras* Foerste, 1936), gyroconic (e.g., *Aphyctoceras* Zhuravleva, 1974) and breviconic conchs (e.g., *Clathroceras* Spath, 1934) and only rarely true ribs, even sometimes very strong (*Epadrianites* Schindewolf, 1931). This type of ornamentation does not seem linked to the morphology of the ammonoid conch, since it concerns platycone shapes, spherococones, involutes with an ogival section, serpenticocones, etc., which can also be extended to other ectocochleate cephalopods, as it includes orthoconic (e.g., *Kionoceras* Hyatt, 1884), cyrtococonic (e.g., *Calocyrtoceras* Foerste, 1936), gyroconic (e.g., *Aphyctoceras* Zhuravleva, 1974) and breviconic conchs (e.g., *Clathroceras* Foerste, 1926). In the Triassic, this trend seems to become less common (*Euflemingites* Spath, 1934, *Chiotites* Renz & Renz, 1948, *Orientosirenites* Konstantinov, 2018, or *Dionites* Mojsicovics, 1893), to become increasingly rare beyond the...
Early Jurassic and to disappear completely before the Late Jurassic. In the Early and Middle Jurassic, spiral ornamentation may be present for oxycone conch morphologies (Amaltheus de Montfort, 1808, Strigoceras Quenstedt 1886), more or less depressed (Phlycticeras Hyatt 1893), but always involute (Liparoceras Hyatt 1867); we can also note the sometimes presence of longitudinal ornamentation on the wrinkle layer in some Oppeliidae (Mironenko, 2015, [1], fig. 12a,b).

For the Cretaceous, we could mention the case of Elobiceras Spath, 1922 with its very distinct spiral notching, which mimics spiral ornamentation. However, it is actually discontinuous and not built on the same model as the previous examples. This is the same for the Cenomanian Forbesiceras Kossmat, 1897 with secondary ribs very projected forward, to the point that it mimics longitudinal ornamentation: until now, this type of ornamentation has, to our knowledge, never been reported for Cretaceous ammonites, with the sole exception of a specimen of Valanginites nucleus (Roemer, 1841) figured by Ploch ([2] 2003, pl. 2, fig. 1). The specimen in question shows a very low-profile series of longitudinal lirae (not a true costal ornamentation), but this character was neither discussed nor reported by Ploch.

The present work focuses on a pattern of longitudinal ornamentation recently discovered in several ammonites from the Valanginian of South-Eastern France. These ammonites (here described as Altudostephanus longicostis gen. et sp. nov.) present a very particular character association which, to our knowledge, has never been described for this stage. The study of their morphology and their suture line allows them to be placed in a precise phylogenetic context within the Olcostephanidae Haug, 1910, and the discovery of the same ornamental pattern in an abnormal Jurassic ammonite (Perisphinctidae Steinmann, 1890) allows us to propose hypotheses to explain its possible origin.

2. Geological Setting

During the Valanginian, the extreme North-Western Tethys (Alpine Ocean) was a large subsident intracratonic area characterized by pelagic sedimentation, known as the Vocontian Basin (Figure 1—South-Eastern France). The deposits show mainly thick marlstones alternated with thinner marly limestone beds. Those beds are more frequent in the lower part of the stage and at its top, whereas the marlstones dominate at the boundary between the lower and upper Valanginian.

Several sections were studied in the southern part of the Vocontian Basin, near the Valanginian hypostratotype (Angles, Alpes de Haute-Provence department—Busnardo et al. 1979 [3]). The specimens studied in the present work are all from the Moriez area in the vicinity of the town of Saint-André-les-Alpes (red star in Figure 1).

The field work was conducted in the protected perimeter of the Geological National Nature Reserve of Haute-Provence that ensures the conservation of the exceptional geological heritage of this territory under French protective laws (see Bert et al., 2022 [4]).

Section PIG5

Several Valanginian sections near Moriez (Vallée de l’Asse) were reported by Thieuloy (1977 [5]; Thieuloy in Busnardo et al., 1979 [3]) as complementary sections of the Valanginian hypostratotype of the Angles road: the Sources de l’Asse and Saint-Firmin sections (here, PIG5—Figure 2). This area was then studied by Bulot (1990, p. 28 [6]) who gave a list of faunas around the lower/upper Valanginian limit, then a partial profile (Bulot, 1995 [7], figs. 10 and 56). The latter author proposed the Saint-Firmin section as a reference for the Karakashiceras inostranzewi Zone (Bulot, 1995, p. 74 [7]) and for the Saynoceras verrucosum Interval Horizon in association with the Angles hypostratotype section (p. 77). He also recognized the ‘Tetrad’ (p. 74) reported for the first time by Thieuloy [5] (1977—T1–T4 in Figure 3), which is an excellent lithological marker present throughout the Vocontian Basin (Reboulet, 1995 [8]). The section is cited again one last time by Bulot and Thieuloy (1994 [9]) and it does not seem to have been restudied since the present work despite its reference status.
Figure 1. Paleogeographic map of the Vocontian Basin for the Valanginian (South-Eastern France). The star points out the sections mentioned in the text in the Moriez area.

In the Asse de Moriez Valley, the Lower Cretaceous outcrops over large areas. In particular, it is possible to follow the beds’ succession in several ravines from the terminal Jurassic (Tithonian) to the lower Aptian. The Valanginian offers the best observation conditions due to sparse ‘badlands’ vegetation. The Saint-Firmin section (PIG5), and to a lesser extent the Sources de l’Asse section (here, section C7), with the same lithology, are the most favorable and allow the beds to be followed continuously for over more than 1 km distance with minimal synsedimentary disturbance. The PIG5 section starts in the lower Valanginian *Busnardolites campylotoxus* Subzone and continues until the upper Valanginian *Criosarasinella furcillata* Zone. The lower/upper Valanginian boundary is particularly well exposed there (Figure 3). The Tetrad and the overlying very marly *Saynoceras verrucosum* Subzone are perfectly recognizable. The proximity of this section from the Angles hypostratotype (6 km in a straight line) and the great stability of the lithology throughout this area make it possible to correlate the two sections bed by bed.
The choice was thus made to keep the Angles numbering for PIG5 (taken from Martinez, 2013 [10]), the less precise one of Bulot (1995 [7]) being recalled (‘B.’ quotation in Figure 2).

**Figure 2.** Log of the section PIG5 in the Moriez area (South-Eastern France) with the repartition of the species at the lower/upper Valanginian boundary.
Figure 3. The section PIG5 with the ‘Tetrad’ beds (T1–T4) topped by the marly area of the *Saynoceras verrucosum* Zone, marking the lithological mark at the upper Valanginian basis.

In the interval studied (beds 303d–306b1—Figure 2), ammonites are most often preserved in the form of small, sometimes very abundant, ‘pyritic’ s.l. nuclei. The index species *Saynoceras verrucosum* (d’Orbigny, 1841) is present (Figure 4), almost continuously between levels 304-1m and 306a6, but it is only really abundant between levels 306am and 306a5. The specimens of *Altudostephanus longicostis* gen. et sp. nov. studied herein come from levels 303d, at the top of the *Neocomites platycostatus* Subzone, 306am, and 306a5m at the base and towards the middle of the *Saynoceras verrucosum* Subzone, respectively.

Figure 4. *Saynoceras verrucosum* (d’Orbigny, 1841); (a) specimen DBT.BK34; (b) specimen DBT.BK30; both are from section PIG5, bed interval 306am–306a3 (Moriez area, South-Eastern France), *Saynoceras verrucosum* Subzone.
3. Material and Methods

Acronyms. RHP = Geological National Nature Reserve of Haute-Provence (Digne-les-Bains, France); MNHN = National Natural History Museum (Paris, France).

Abbreviations. D = diameter; H = whorl height; W = whorl width; U = umbilic size; N1/2 = number of ribs on the flanks per half-whorl; N2/2 = number of longitudinal ribs on the half-venter; c. means that the value is estimated.

3.1. Material and Its Conservation

The present work focuses on extremely rare bed-by-bed sampled ammonites, here *Altudostephanus longicostis* gen. et sp. nov. All the collected material is curated by a public institution (RHP). The photos of the ‘pyritic’ specimens were taken with an X2 macro lens; the other larger specimens were photographed with an X1 standard macro lens.

As the studied fossils are preserved in the form of ‘pyritic’ s.l. nuclei (‘iron sulphide-containing’, following Rouchon et al., 2011 [11]), they are likely to deteriorate over time more or less quickly because of the chemical reactions involved in pyrite oxidation/hydration (Larkin, 2011 [12]; Tacker, 2020 [13]).

Pyrite is usually extremely stable over time in reduced conditions inside the sediments (protected from oxygen). During the erosion process, the fossils come over the surface and are exposed to aerobic conditions, all the more oxidizing in the presence of water (rain), newly-formed salts from marls (gypsum), acidic environment and chemolithoautotrophic bacteria (on the sulphides), which catalyze the reactions, ultimately leading to part of an electrochemical process. The oxidation of pyrite is usually traced by the simplified chemical equation (Pyrit: FeS$_2$; Iron sulphate (II) (ferrous): FeSO$_4$; Sulphuric acid: H$_2$SO$_4$):

$$4\text{FeS}_2 + 13\text{O}_2 + 2\text{H}_2\text{O} \rightarrow 4\text{FeSO}_4 + 2\text{H}_2\text{SO}_4 + 2\text{SO}_2$$

Sulphuric acid is a strong acid that dissociates nearly completely in water and is usually considered as the culprit in specimen destruction. Also, low pH generates Fe$^{3+}$, which can also induce an oxidation reaction with ‘pyrite’:

$$\text{FeS}_2 + 14\text{Fe}^{3+} + 8\text{H}_2\text{O} \rightarrow 15\text{Fe}^{2+} + 2\text{SO}_4^{2-} + 16\text{H}^+$$

The additional importance of the presence of impurities in the pyrite instability process has been explored by Schronk (2023) [14]. Finally, the volume of the products is much larger than those of the initial ‘pyrite’, resulting in volumetric expansion. Such expansion is likely to accelerate the process of specimen degradation through the production of cracks, which increases the permeability to moisture and acids directly in areas of the specimen that were previously sheltered, the result of these processes being the final disintegration of the specimen.

Treatment protocols to prevent ‘pyrite’ deterioration have been used historically, with varying degrees of success (see e.g., Newman, 1998 [15], Larkin, 2011 [12] and Schronk, 2023 for a review [14]), but they are often toxic or require special conditions difficult to implement, in particular for a large number of specimens to be treated in series (dry ammonia gas, ethanolamine thioglycollate, vacuum-packaging, etc.).

From all the studies on the question of the conservation of ‘pyritic’ specimens in paleontology, it appears that preventive treatment is the best option. In all cases (preventive as well as curative), a certain number of steps must be respected, which allows us to detail the protocol implemented in this work:

1. Cleaning the specimens with water makes it possible, on the one hand, to eliminate labile mineral species by conditioning with water (these are mainly oxidized species such as hydrated ferric sulphates Fe$_2$(SO$_4$)$_3$, $n$ H$_2$O with 0 < $n$ < 9—Sorrenti, 2007 [16]), and on the other hand, to remove mechanically any trace of powdery alteration with a fine brush. It is followed by complete passive drying;
2. Neutralization of the effects of oxidation was performed using an acid (Newman, 1998 [15]): here, the choice was made to place the specimens in a bath of 20% water-
diluted phosphoric acid at room temperature \((H_3PO_4—Prytulak, 1991 [17])\). The duration of the bath is 24–48 h depending on the response of the specimens (regular visual inspection). It allows the removal of the oxidation by-products; especially, the \(PO_4^{3−}\) molecule reacts with Fe\(^{3+}\) on the pyrite surface (Evangelou, 1995 [18]; Evangelou and Zhang, 1995 [19]; Elsetinow et al., 2001 [20]), and here the phosphate molecule also acts to passivate the Fe\(^{3+}\). This step is followed by rinsing the specimens under running water with a fine brush, in order to remove any loosened rust and to thoroughly neutralize the excess phosphoric acid, including in the cracks. Any possible powdery parts that disintegrate are removed again. Rinsing is followed by complete passive drying;

3. Passivation of the specimens: treatment by passivation with humic acid use was recommended by Belzile et al. (1997) [21], which involves coating the specimens with a substance that renders them impenetrable to oxidative attack. Passivating the surface of the ‘pyrite’ with organic molecules makes it possible to inhibit the surface chemical reactivity of the mineral (adsorption). Here, we have chosen passivation with tannic acid water diluted to 10% (Prytulak, 1991 [17]), which is a non-toxic and practical product to use. Thoroughly dry specimens are soaked for several seconds to tens of seconds in the tannic acid solution, ensuring that the product penetrates everywhere into the cracks. Tannic acid \((C_{76}H_{52}O_{46})\), in contact with the ferric ion Fe\(^{3+}\), is transformed into tannate iron (III) \(Fe_2(C_{14}H_{7}O_9)(OH)_3\). This step is followed by complete passive drying by turning the specimens regularly to avoid any accumulation of tannic acid by gravity. An observation phase lasting several days, or even weeks, will ensure that the deterioration process does not resume. Any recovery must be processed again from step 2;

4. Installation of the gas-proofing barrier: wax-based products, as well as liquid thermosetting resins, have yielded poor results and age poorly over time. They can crack under the effect of the contraction/expansion of the ‘pyrite’ with temperature differences, which does not make them perfectly impermeable to gases, with the risk that the degassing of these products would eventually produce oxidizers to further degrade the pyrite surface (Tacker, 2020 [13]). In addition, the thickness of the coating provides a glossy finish, coating the finest details of the specimens and making them barely visible for subsequent studies (Figure 4a; Larkin, 2011, p. 41 [12]). Treatment by encapsulation with phospholipids yields good results by protecting the specimens from oxygen, provided that they are totally immersed into the lipid fluid: the hydrophobic pocket in the bilayer lipid structure can inhibit the interaction of water with the pyrite surface and hence inhibit or suppress the deterioration process (Kargbo et al. 2004 [22]). This technique, although it stops oxidation by 90%, does not allow treatment of damaged areas on its own. It can also be complicated to be implemented in the conservation conditions of collections and hinders the subsequent handling of specimens and labels. The use of silicone seems to yield good results for stabilized specimens; it is also inert, impermeable to air and non-hazardous (Collinson et al. 2016 [23]; Newman, 1998 [15]; Fenlon and Petrera, 2019 [24]), but it dries slowly. As an alternative, we recommend treatment with residue-free Polytetrafluoroethylene (PTFE), which has the advantage of being quick-drying. Just like silicone, it has significant oxygen and moisture barrier capabilities. The use of PTFE also has a practical side by allowing the study and easy handling of treated specimens once dry. Their interest lies in the presence of fluorine in the molecules, this element providing the polymer a greater chemical stability and high resistance to ultraviolet rays, without drying shrinkage (Bromblet, 2002 [25]). Complete drying is achieved after a period of several days;

5. Of course, this preventive/curative protocol does not preclude ensuring long-term conservation of the treated specimens in a place protected from humidity and temperature variations. The use of silica gel desiccants is also recommended, as well as the implementation of a collection survey protocol. Finally, producing of replicas or
CT- or 3D-surface scans would ensure that the morphology is conserved, even if the specimens deteriorate despite all efforts.

3.2. Stratigraphy

The biostratigraphic framework used here is the one proposed by the I.U.G.S Lower Cretaceous ammonite working group, the Kilian Group (Szives et al., 2023 [26]), recalled in Table 1.

Table 1. Biostratigraphic framework for the Valanginian. Black cells show the species repartition.

<table>
<thead>
<tr>
<th>Stages</th>
<th>Zones</th>
<th>Subzones</th>
</tr>
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<tbody>
<tr>
<td>Barronites hirsutus (Fallot et Termier, 1923)</td>
<td>Altudostephanus josephinus gen. nov.</td>
<td>Altudostephanus longicostis gen. et sp. nov.</td>
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<tr>
<td>Altudostephanus longicostis gen. et sp. nov.</td>
<td>Olcostephanus stephanophorus (Matheron, 1878)</td>
<td>Olcostephanus temnitheycheletulae Bulot, 1905</td>
</tr>
<tr>
<td>Olcostephanus stephanophorus (Matheron, 1878)</td>
<td>Olcostephanus drumensis Kilian, 1910</td>
<td>Olcostephanus murneri Roemer, 1841</td>
</tr>
<tr>
<td>Olcostephanus drumensis Kilian, 1910</td>
<td>Valanginian nucleus (Roemer, 1841)</td>
<td></td>
</tr>
</tbody>
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4. Systematic Palaeontology

Class Cephalopoda Cuvier, 1798
Order Ammonoida Haeckel, 1866
Suborder Ammonitina Hyatt, 1889
Superfamily Perisphinctoidea Steinmann, 1890
Family Olcostephanidae Haug, 1910
Subfamily Olcostephaninae Haug, 1910
Genus Altudostephanus gen. nov.

Etymology. Related to its morphological convergence with the Permian (Guadalupian) ammonoid genus Altudoceras Ruzhentsev, 1940, both having similar constrictions, lateral
adoral oriented ribs, and ventral spiral true ribs. Also related to the phyletic position among the Olcostephaninai.

**Zoobank Record.** LSID urn:lsid:zoobank.org:act:DCCE1C62-57DA-45E6-8BEC-5B3C716D855D.

**Type species.** *Altudostephanus longicostis* gen. et sp. nov.

**Species included.** *Altudostephanus longicostis* gen. et sp. nov. and *Altudostephanus josephinus* (d’Orbigny, 1850 [28]). Note that the latter species was introduced by d’Orbigny in his *Prodrome* (1850) based on a single specimen (see Cottreau, 1934, p. 50 [29]). This specimen (MNHN.FR03115) is thus the holotype by monotypy. Another specimen (MNHN.F.A00067) is indicated as being a syntype of the species by the MNHN (https://science.mnhn.fr/institution/mnhn/collection/I/item/a00067, accessed on 10 April 2024). We disagree with this attribution for the following reasons:

- This latter specimen was not mentioned by Cottreau in the revision of the *Prodrome* types, who explicitly stated that one single specimen was attributed to this species by d’Orbigny (4861, now MNHN.F.R03115). As this is the only specimen, then this is unquestionably the holotype and there cannot be any other syntypes, according to the rules of the ICZN;
- Its morphological characters (radial primary ribs; secondary ribs thin and well expressed on the ventral area; absence of the angular shoulder forming a ledge at the termination of the primary ribs; constrictions much rarer; prominent and rounded tubercles) do not allow assigning the specimen MNHN.F.A00067 to *A. josephinus*;
- It is indicated that the specimen MNHN.F.A00067 comes from Saint-Julien-en-Beauchêne, a locality situated in the northern part of the Vocontian Basin (northwest of Veynes in Figure 1). This is definitely not the case: the obvious presence of glauconite in the matrix and its light beige phosphate limestone allow us to affirm without ambiguity that it comes from the area of drowned platforms surrounding the Vocontian Basin. This type of preservation is known, for example, in the Arc de Castellane to the south of the basin (Cotillon, 1971 [30]);
- Bulot (1990, 1995 [6,7]), then more recently Kenjo (2014) [27], showed that *A. josephinus* gen. nov. is present only in the lower Valanginian (see below the stratigraphic occurrence). However, fossils with the same preservation as specimen MNHN.F.A00067 are known on platform edges in significantly higher levels, near to the boundary between the Valanginian and the Hauterivian (e.g., Autran, 1993 [31]);
- All the previous points allow us to consider the specimen MNHN.F.A00067 as *Olcostephanus balkanicus* (Tzankov, 1942).

**Geographic and stratigraphic occurrences.** The genus is currently only known in the southeast of France, in the southern part of the Vocontian Basin, from the base of the *Neocomites neocomiensiformis* Zone (see Kenjo, 2014 [27], figs. 1 and 4; =*Barronites hirsutus* Interval Horizon in Bulot, 1995 [7]) to the base of the *Saynoceras verrucosum* Zone (*S. verrucosum* Subzone).

**Diagnosis.** Cadiconic shell, evolute, with a large crateriform umbilicus and a very broad and slightly convex venter. The oblique periumbilical area merges with the flanks, which pass to the ventral area via an angular shoulder forming a ledge. Irregular primary ribs exclusively present on the flanks, curved concavely forward in their lower part, proverse at their apex and reinforced by a punctiform tubercle on the angular ledge. Secondary ribs present exclusively ventrally, starting from the lateral tubercle in bundles of 3–4. They can be turned upside down perpendicularly and, in this case, form a longitudinal ornamentation in the direction of the coiling. Frequent constrictions: concave forwardly on the flanks (identical outline as primary ribs), and very convex forwardly on the venter, regardless of the orientation of the ribs. Suture line of general olcostephanide type (formula IU₂LE), but very simplified with deep and slightly indented elements.

**Discussion.** *Altudostephanus* gen. nov. has morphological affinities with *Olcostephanus* species with very depressed sections. However, the crateriform aspect of the umbilicus (wider), the presence of the angular ledge and the almost flat ventral area are discriminating
criteria. In Altudostephanus gen. nov., the flanks are merged with the periumbilical area and the venter is well individualized, whereas in Olcostephanus it occupies more space and the periumbilical area is well defined. The systematic presence of a well-marked longitudinal ornamentation in the form of true ribs in at least one species (A. longicostis gen. et sp. nov.) is also an important characteristic, while it is absent in Olcostephanus (e.g., O. tenuituberculatus Bulot, 1990 [7]—Figure 5a), even if lirae can be exceptionally observed (O. stephanophorus (Matheron, 1878)—Figure 5b). Finally, the suture line is most often simpler with considerably less indented elements.

Compared to Valanginites Kilian, 1910 (Valanginites nucleus (Roemer, 1841)—Figure 5c), Altudostephanus gen. nov. has a significantly less globular morphology, the venter being slightly convex only. The constrictions are also more frequent, better marked and clearly more pronounced on the ventral area. The proverse primary ribs (and not radial as in Valanginites) are also better marked in Altudostephanus gen. nov., where they bear a punctiform tubercle very early during ontogeny, whereas in Valanginites, the tuberculation appears later (Ploch, 2003 [2]), when it exists, sometimes expressed on the siphonal zone, which is never the case in Altudostephanus gen. nov. Just as in Olcostephanus, the presence of longitudinal ornamentation in the form of lirae is only exceptional in Valanginites and never

Figure 5. (a) Olcostephanus tenuituberculatus Bulot, 1990, specimen DBT.BX31; (b) Olcostephanus stephanophorus (Matheron, 1878), specimen DBT.BK33, the arrows show longitudinal lirae; (c) Valanginites nucleus (Roemer, 1841), specimen DBT.BK32; (a,c) are from the section PIG5 in the Moriez area, (b) is from the Lioux area near Barrême (South-Eastern France), all from the Saynoceras verrucosum Subzone.
as the true costulation found in *Altudostephanus* gen. nov. (*A. longicostis* gen. et sp. nov.). Finally, the suture line is always simpler and less indented in *Altudostephanus* gen. nov.

Faraoni et al. (1997) [32] described an ammonite with an unusual shape for the lower Valanginian “Thurmanniceras” pertransiens Zone: *Cantianiceras* Faraoni et al., 1997. Compared to *Altudostephanus* gen. nov., the former is more compressed with tabulate flanks, well-defined periumbilical area, bi-tuberculate (which is never the case in the latter) and with rarer constrictions.

*Altudostephanus longicostis* gen. et sp. nov.

Figure 6a–c

![Figure 6. Altudostephanus longicostis gen. et sp. nov. (a) specimen DBT.BK35 (holotype), section/bed PIG5/306a5m in the Saynoceras verrucosum Subzone of Moriez; (b) specimen DBT.AU38, section/bed C7/306am in the Saynoceras verrucosum Subzone of Moriez; (c) specimen DBT.BK36, section/bed PIG5/303dm in the Neocomites platycostatus Subzone of Moriez; (d) Altudostephanus josephinus gen. nov., specimen MNHN.F.R03115 (holotype), from the Saint-Julien-en-Beauchêne area (Hautes-Alpes, South-Eastern France), curated at the MNHN (photography by RECOLNAT, Peter Massicard).](image)

**Etymology.** Because of the systematic presence of longitudinal ribs on the ventral area.

**Zoobank Record.** LSID urn:lsid:zoobank.org:act:30ED61DB-355A-465E-9AD9-E7EE5C050B74
**Holotype.** Specimen DBT.BK35.

**Type locality.** Section PIG5, near Saint-Firmin (Moriez area, Alpes-de-Haute-Provence department, South-Eastern France).

**Type horizon.** Bed 306-5am of the type section.

**Geographic distribution.** Species currently known only in the south of the Vocontian Basin (southeast of France), in the Moriez area close to the Valanginian hypostратotype.

**Stratigraphic distribution.** *A. longicostis* gen. et sp. nov. is found around the lower/upper Valanginian boundary, from the top of the *N. platycostatus* Subzone (*K. inostranzewi* Zone) to the middle part of the *S. verrucosum* Subzone (*S. verrucosum* Zone).

**Diagnosis.** Cadiconic evolute shell with a large crateriform umbilicus and a very broad and slightly convex venter. The oblique periumbilical area merges with the flanks, which pass to the ventral area via an angular shoulder forming a ledge. Irregular primary ribs, frequent and exclusively present on the flanks, concave forward in their lower part, proverse in their upper part then reinforced by a punctiform tubercle on the angular ledge. Secondary ribs reversed perpendicularly forming a longitudinal ornamentation in the direction of the coiling. Frequent constrictions: concave forward on the flanks (identical outline as primary ribs), and very convex forward on the venter. Suture line of general olcostephanide type (formula IU$_2$LE), but very simplified with deep and slightly indented elements.

**Material studied.** Three small ‘pyritic’ specimens from the Moriez area: DBT.BK35 (the holotype), DBT.BK36, the both from section PIG5 (respectively, from beds 306a5m and 304-2m), and DBT.AU38 from section C7 (bed 306a).

**Measurements.** See Table 2.

**Table 2.** Measurements of the specimens. All measures are in mm.

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Section/Level</th>
<th>D</th>
<th>H</th>
<th>W</th>
<th>U</th>
<th>H/D</th>
<th>W/H</th>
<th>U/D</th>
<th>U/H</th>
<th>N1/2</th>
<th>N2/2</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBT.BK35</td>
<td>PIG5/306a5m</td>
<td>12.74</td>
<td>5.00</td>
<td>8.32</td>
<td>4.28</td>
<td>0.39</td>
<td>1.66</td>
<td>0.34</td>
<td>0.86</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>DBT.BK36</td>
<td>PIG5/304-2m</td>
<td>10.80</td>
<td>3.46</td>
<td>6.26</td>
<td>3.60</td>
<td>0.32</td>
<td>1.81</td>
<td>0.33</td>
<td>1.04</td>
<td>?</td>
<td>7</td>
</tr>
<tr>
<td>DBT.AU38</td>
<td>C7/306a</td>
<td>19.08</td>
<td>7.16</td>
<td>-</td>
<td>7.48</td>
<td>0.36</td>
<td>-</td>
<td>0.39</td>
<td>1.05</td>
<td>14</td>
<td>?</td>
</tr>
</tbody>
</table>

**Description of the specimens.** Three specimens are studied, all being fully septate without the sutures showing any approximation, and they do not seem to show any signs of maturity. The largest specimen (DBT.AU38; Figure 6b) is compressed post-mortem; the smallest (DBT.BK36; Figure 6c) is fragmentary, but allows good examination of the section.

The shell is cadiconic evolute (0.33 < U/D < 0.39). The umbilicus is wide and crateriform and the absence of a clearly defined umbilical wall means that the oblique periumbilical area is merged with the flanks. The venter is very broad and slightly convex (1.66 < W/H < 1.81); it is connected to the ventral area via an angular shoulder forming a ledge at the maximum thickness of the section. Those features give a very characteristic appearance to the shell. At least two ontogenetic stages are known:

- The innermost whorls, up to approximately D = 0.7 mm, are smooth on the flanks (the venter is not visible at this diameter on the specimens studied) and have no visible ornamentation apart from the constrictions (see below);
- The rest of the known shell (Dmax = 19 mm) shows an ornamentation consisting in primary ribs, relatively frequent (9–14 per half-whorl), but irregularly spaced. On the flanks, they are concave towards the aperture in their lower part, then proverse in their upper part. At the angular ledge between the flanks and the venter, the primary ribs are reinforced by a nodular punctiform tubercle. The ledge of the angular shoulder therefore shows an irregular crenulated appearance. Very faint constrictions are visible from time to time along the same line. Their number and vigor are very irregular and they are generally associated with the primary ribs that they precede. On the venter, where they are better marked and bordered by faint ridges, they continue their
proximal projection so as to present a strong concavity towards the rear of the shell at the siphonal area. Transverse striae irregular pattern is also present with the same path (DBT.BK35). Conversely, the primary ribs diminish considerably on the venter where they are only evanescent and difficult to perceive. The most striking aspect of the ornamentation consists of the presence of secondary ribs reversed perpendicularly to the primary ribs, thus forming a longitudinal ornamentation in the direction of the coiling. These ribs are slightly wavy at the intersection of the primary ribs. There are 7 longitudinal ribs per half of the ventral area in specimens where it is sufficiently preserved (i.e., 14 over the entire ventral area). This longitudinal ventral pattern appears smoothly from $D = 7$ mm, whereas at his diameter the constrictions, there ridges, and megastriae (when present) are fully expressed.

The suture line is of olcostephanid type (IU$_2$LE formula), but very simplified, with deep external elements and remarkably little indentation, to the point that the terminal aspect of the lateral lobe is poorly defined. The external saddle and the ventral lobe E have almost no secondary indentations. The ventral lobe is distinctly bifid with deep terminal phylites.

**Systematic discussion.** The general morphology of the shell of *A. longicostis* gen. et sp. nov. can only be validly compared with that of *A. josephinus* gen. nov. from the lower Valanginian. Both species have very strong similarities, such as the cadiconic appearance of the shell with the characteristic crateriform shape of the umbilicus, the periumbilical area merging with the flanks and the slightly convex venter. The angular ledge joining the flanks to the venter is more pinched in *A. longicostis* gen. et sp. nov. Ornamentation is also comparable between both species. However, the primary ribs appear longer on the flanks and less marked on the venter in *A. longicostis* gen. et sp. nov. The constrictions have a less marked concavity on the venter in *A. josephinus* gen. nov., and above all, in the latter, the secondary ribs are perpendicular to the direction of coiling and never longitudinal as in *A. longicostis* gen. et sp. nov. This latter point is the most discriminating character of the new species. The suture line, although also very simplified in *A. josephinus* gen. nov., is a little more indented, particularly the external saddle and the ventral lobe E.

*A. longicostis* gen. et sp. nov. is morphologically quite different from the contemporary *Olcostephanus* species, including those with very depressed sections (*O. tenuituberculatus* and especially *O. stephanophorus*). The wide and crateriform umbilicus with the presence of the angular ledge connecting the flanks to the ventral area are not usual characters in *Olcostephanus* whose shells are often rather globular with a relatively closed umbilicus (Figure 5a,b). In *Olcostephanus*, the ornamentation is also very different, the primary ribs being short, nodular at the point of bifurcation, and the well-marked secondary ribs cross the venter perpendicular to the direction of the coiling of the shell, without forming longitudinal lines. Exceptionally, lirae can be observed in *O. stephanophorus* (Figure 5b), but apart from their longitudinal direction, they are anecdotal and have nothing to compare with the true secondary ribs of *A. longicostis* gen. et sp. nov. Finally, in the latter, the suture line is simpler with elements that are always less indented, even compared to *O. stephanophorus*.

*Valanginites nucleus* (Figure 5c) is clearly always more globular than *A. longicostis* gen. et sp. nov. In the latter, the constrictions are more frequent and better marked, more inclined forward on the venter. The primary ribs are also better marked in *A. longicostis* gen. et sp. nov. where they bear a punctiform tubercle very early during ontogeny: when present, the tuberculation appears later in *V. nucleus*, sometimes including in the siphonal zone, an area where it is never expressed in *A. longicostis* gen. et sp. nov. Just as in *O. stephanophorus*, the presence of longitudinal ornamentation is exceptionally rare in *Valanginites* and only in the form of lirae. Finally, the suture line is always simpler and less indented in *A. longicostis* gen. et sp. nov., with U$_2$ clearly less well individualized.

*Cantianiceras cantiense* Faraoni et al., 1997 and *C. dieuse* (Sayn, 1889) also have an unusual shape for the lower Valanginian “Thurmanniceras” *pertransiens* Zone, with a very evolute conch and a strong ornamentation. However, compared to *A. longicostis* gen. et sp. nov.
et sp. nov., both are more compressed with tabulate flanks, well-defined periumbilical area, rarer constrictions, and above all, they are bi-tuberculate, which is never the case in *Altudostephanus* gen. nov.

5. Discussion

The presence of longitudinal ribs on a Valanginian ammonite raises questions due to its resemblance to features usually found in Palaeozoic or old Mesozoic taxa. The regularity of the phenomenon, its systematic presence in all specimens of *Altudoceras* gen. nov. around the lower/upper Valanginian boundary, and its symmetry exclude any mechanical reason, pathological or parasitic-type phenomena described to date in ammonites (de Baets et al., 2015 [33]; Keupp, 2012 [34]; Hoffmann and Keupp, 2015 [35]). With several specimens having been collected, all with the same morphology, in a relatively constrained stratigraphic and geographical interval, there is no doubt for us that this is not an ‘accident’ but rather the feature of ‘a true biological species’, although rare. We consider this pattern as true secondary ribs reverted (homologous character) and not as any other longitudinal pattern which could have other formation mechanism (lirae, striae or megastriae; e.g., Urdy, 2015 [36]): this longitudinal pattern appears smoothly during ontogeny in the same way as secondary transverse ventral ribs in other Olcostephanid species (see description chapter and e.g., Figure 5a,b); it replaces the secondary ribs pattern, which totally disappears compared to other Olcostephanid species, including *A. josephinus*. Regarding this disappearance, we exclude any taphonomic bias due to the homogeneity of the ‘pyritic’ fossils’ preservation.

The definition of a systematic/evolutionary framework for *A. longicostis* gen. et sp. nov. is absolutely necessary to propose hypotheses about this surprising character. The very close morphological proximity between *A. longicostis* gen. et sp. nov. and *A. josephinus* gen. nov., apart from the longitudinal reversal of the ventral ribs, allows us to consider a close phyletic link between both species, in the sense *A. josephinus* gen. nov.→*A. longicostis* gen. et sp. nov., a link reinforced by their respective stratigraphic distribution (Table 1).

*A. josephinus* gen. nov. was studied by Bulot (1990 [6]), who proposed a possible origin of this species from *Olcostephanus drumensis* (considered to be the ancestral species of the more recent *Olcostephanus*), or even from *O. stephanophorus*, evoking in both hypotheses speciation by progenesis (Dommergues et al., 1986 [37]). This hypothesis is well supported by the drastic simplification of the suture line and the existence of specimens with intermediate features between these species (Bulot, 1990 [6], pl. 2, figs. 3–6 and 15). If we retain the possibility of progenesis, the existence of specimens of *O. drumensis* with a cadiconic section in the inner whorls seems to us an additional argument for a phyletic relationship with *A. josephinus* gen. nov. Under these conditions, the clade formed by *A. josephinus* gen. nov. and *A. longicostis* gen. et sp. nov., for which no descendants have been proposed to date, is monophyletic and justifies its new genus status within the Olcostephaninae.

Concerning the longitudinal ribs feature, the discovery of the same ornamental pattern in a very exceptional Oxfordian (Upper Jurassic) specimen of *Passendorferia* Brochwicz-Lewinski, 1973 from the Nevers area (Nièvre department, central-east of France), which just like the Olcostephanidae belongs to the superfamily Perisphinctoidea Steinmann, 1890, provides interesting insight. This specimen, unique to date (Figure 7a), has certain peculiarities which must be highlighted: neither the coiling nor the ornamentation of the lateral part of the shell are affected by the anomaly, which are therefore very comparable with the ‘normal’ shell known from *Passendorferia* (Figure 7b). Thus, the primary ribs adopt the expected layout for a representative of this genus. The constrictions are also not affected and are expressed normally, including on the ventral area, as observed in *A. longicostis* gen. et sp. nov. compared to *A. josephinus* gen. nov. However, the secondary ribs are reversed (no other transverse rib-like pattern is visible) and adopt a course parallel to the coiling, identical to that observed in *A. longicostis* gen. et sp. nov. It is interesting to note that the resemblance of this feature between both species achieves great details, which weakens the
hypothesis of a simple convergence: termination of the primary ribs is slightly reinforced, exactly as observed in *A. longicostis* gen. et sp. nov.

These similarities call for a certain number of remarks. First of all, they allow thinking that the mechanisms involved in what we assume to be a ‘reversal’ of the ribs are the same for both species, despite their stratigraphic and phyletic distance (although with a ‘common stock’ Perisphinctoidea). Then, the constrictions (and striae in *Altudostephanus* nov. gen.) are not affected by the reversal phenomenon in either case, as their construction process differs from that of the ribs (Urdy, 2015 [36]).

Figure 7. (a) *Passendorferia* sp., specimen DBT.BK29 from the Oxfordian near Nevers (east-center of France) showing an anomaly in the ornamentation: the secondary ribs are longitudinal in the direction of the coiling; (b) *Passendorferia torcalense* (Kilian, 1889), specimen DBT. BK28, from the upper Oxfordian of Haute-Provence (South-Eastern France), the ornamentation shows the ‘normal’ morphology expected for the genus.

The example of *A. longicostis* gen. et sp. nov., where the character ‘longitudinal ribs’ is passed on to the offspring as part of the phenotype of the species, allows us to propose that this ability to reverse the ribs could maybe have a genetic cause (like a switch), linked, for example, to the expression of architect genes. An interesting parallel could be made with suture pseudoinversion; Rogov (2019) [38] considered that in some cases, this abnormality could be related to genetic causes, such as a case of homeotic mutation, possibly caused by transcription errors in polarity genes. The character ‘longitudinal ribs’ is however exceptionally rare within populations beyond the Middle Jurassic (and belonging to other superfamilies or even suborders), to such an extent that its expression becomes an anomaly: in the context of numerically large populations (tending towards the Hardy–
Weinberg theoretical equilibrium, e.g., Lachance, 2016 [39]), as among Passendorferia, a form of standardization tends to take over the random mutations that could be expressed and makes them disappear. For Altudostephanus gen. nov., the situation is very different due to the extreme numerical reduction in the population and its very restricted geographical range compared to its original group (Bulot, 1990 [6]). In this case, the appearance of a rare dominant mutation, or any other genetic cause emerged, for example, by genetic drift, can more easily invade the phenotype of the population as part of a founder effect (e.g., Angst et al., 2022 [40]).

6. Conclusions

The discovery of a new ammonite species around the lower/upper Valanginian boundary (Lower Cretaceous—Altudostephanus longicostis gen. et sp. nov.) with true longitudinal ribs, firstly reported here in the Cretaceous, raises questions as this type of ornamentation is mainly represented in the Paleozoic or old Mesozoic taxa. Its study shows that it is not a ‘shell accident’ and that it belongs to a particular lineage of Olcostephaninae, in a very restricted geographical area and in a progenetic evolutionary context from Olcostephanus, as highlighted by Bulot (1990 [6]), which justifies the introduction of the new monophyletic genus Altudostephanus gen. nov.

Compared to its parent species, A. josephinus gen. nov., the secondary ribs of A. longicostis gen. et sp. nov. are literally reversed at 90°. Comparison of this phenomenon with a unique specimen of Passendorferia from the Oxfordian (Upper Jurassic) presenting the same reversal allows us to consider that the construction of the ornamentation process is identical in both cases, which possibly suggests a genetic cause (sensu lato) for this phenomenon. The absence of normal secondary ribs replaced with the longitudinal pattern, presence of termination of the primary ribs slightly reinforced in the same way for A. longicostis gen. et sp. nov. and the specimen of Passendorferia sp., and absence of ribs with an intermediate orientation (like, for example, what is known in the Cenomanian Forbesiceras with very projected forward secondary ribs pattern) allows us to think, as a hypothesis, that in the present case, a set of genes could act as a ‘switch’, which would modulate the orientation of the ribs in one direction or the other (rare dominant mutation on architect genes?). A possible interpretation could be that this set would have ceased to be expressed over time in most groups of ammonites since the beginning of the Mesozoic, except in the Perisphinctoidea where it would, however, have become strongly recessive. Its possible accidental expression in populations (e.g., Passendorferia) would have been more or less effectively absorbed and masked by genetic mixing (Hardy–Weinberg theoretical equilibrium) and this character would thus not have been transmitted to descendants, except in Altudostephanus longicostis gen. and nov. thanks to a possible genetic drift and the founder effect in a drastic population reduction.

It is interesting to note that the phenomenon of progenesis, associated with the appearance of Altudostephanus gen. nov., is often invoked to be the cause of radical changes causing ruptures in evolutionary continuities and therefore to new lineages (e.g., Dommergues et al., 1986, p. 354 [37]). But here, the appearance of the very original character of reversed ribs did not seem to represent a sufficient advantage to stop the unfavorable effect of the drop in diversity on adaptation of the species, which apparently disappeared very quickly after its appearance without leaving any descendants.


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Data Availability Statement: Data is contained within the article.
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